Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE

AMERICAN NATURALIST

VOL. XL *August, 1906* No. 476

VOLANT ADAPTATION IN VERTEBRATES

RICHARD S. LULL

OF THE several environments to which vertebrates have become adapted, the two which most profoundly modify their inhabitants are the water and the air. This is in part due to the fact that a homogeneous environment pressing upon all sides of the organism with almost the same intensity has moulded the form into a symmetrical contour which offers but little resistance in passing through the medium. In addition, special modifications of the limbs must occur, supplemented in air-inhabiting forms by cutaneous expansions or appendages for support or propulsion, without which very existence in the medium is out of the question.

Aquatic life modifies its denizens the more profoundly, because it becomes permanently sustaining, while even the best of fliers must ultimately return to the trees, the earth, or the sea. The aërial forms therefore always retain functional structures to enable them to move in the environment from whence their ancestors came. Of the more perfectly adapted aquatic types this is not true.

Creatures, other than the aquatic forms, can exist in the terrestrial realm without special adaptation; many forms which can climb fairly well may hardly be said to exhibit scansorial modification and indeed, while prolonged life in the water profoundly alters the contours of the animal, many vertebrates are fair swimmers whose proper environment is elsewhere. To venture into the aërial realm without an especial equipment for flight is to court destruction like Darius Green, though many animals which cannot even soar, are wonderful leapers.

With the exception of the Amphibia, every class of vertebrates has developed true flight, while the power of soaring from a higher to a lower level has been acquired again and again.

Altogether no fewer than seventeen separate evolutions for aërial life have occurred among vertebrates, true flight five and probably seven[1] times, and soaring at least ten times. The forms which soar are singularly uniform in the plan of the sustaining mechanism and one would be justified in considering many of the volant mammals as the result of a single evolution were it not for the fact that in many cases the nearest relatives, which might prove annectant, are flightless forms. In true fliers, however, there is in each instance so distinct a plan of structure that there is not the slightest doubt that each has arisen through a separate evolution.

It is necessary to draw a sharp line of demarcation between the soarers and those having true flight, and the latter are again divided according to the mode of progression. These are, to use Marey's terms, the sailers, forms of great wing expanse like the vultures which rise slowly, but once in the air sustain themselves on almost motionless pinions; and the rowers or wing-flappers, such as have limited alar expanse and must make good this lack by a rapid vibration of the wings. This type culminates in the hummingbirds, though including many large birds of great speed as the wild goose. There are also gradational forms between the two extremes. Nor are these two methods confined to the birds, for among the pterodactyls it is evident that both kinds of true flight prevailed. Also, among the bats there are some of rapid wing movement, while others flap slowly, tending toward the sailing method of flight.

While the mode of flight is perfectly apparent in most aërial vertebrates, in some instances it has been difficult to assign the animal to the proper group as in the case of flying-fishes whose method of locomotion has given rise to much argument. Moseley's description of the flight of the albatross (Moseley, '79, p. 570) is another instance of the correction of a popular misconception due to a lack of knowledge of mechanical principles, for while vultures, when sailing, are continually sliding down an inclined plane, the albatross was supposed to sail close to the sea without losing altitude; a manifest impossibility.[1]

---

[1] I am not sure under which head the fossil flying-fishes should come; but unless their fin-wings were far larger proportionately than those of modern types Colonel Durnford's argument would hold good for them as well and would place them among the true fliers (*vide infra* p. 541).

CLASSIFICATION

Volant vertebrates may be classed as follows: —

Evolution			Soaring	Flapping	Sailing
	Pisces				
1	Ganoidei	Thoracopterus		×	
2		Gigantopterus		×	
3	Teleostomi	Exocœtus		×	
4		Dactylopterus		×	
	Amphibia				
5	Anura	Rhacophorus	×		
	Reptilia				
6	Squamata	Ptychozoön	×		
7		Draco	×		
8	Pterosauria	(entire order)		×	×
9	Aves	(entire class)		×	×
	Mammalia				
10	Marsupialia	Ptauroides	×		
11		Petaurus	×		
12		Acrobates	×		
13	Rodentia	Anomalurus	×		
14		Pteromys Sciuropterus Eupetaurus	×		
15	Insectivora	Galeopithecus	×		
16	Chiroptera	(entire order)		×	
17	Primates	Propithecus	×		
	Total		10	7	2

In all 17 evolutions.

---

[1] Moseley says: "I believe that Albatrosses move their wings much oftener than is suspected. They often have the appearance of soaring for long periods after a ship without flapping their wings at all, but if they be very closely watched, very short but extremely quick motions of the wings may be detected. The appearance is rather as if the body of the bird dropped a very short distance and rose again. The movements cannot be seen at all unless the bird is exactly on a level with the eye. A very quick stroke, carried even through a very short arc, can of course supply a large store of fresh momentum. In perfectly calm weather, Albatrosses flap heavily."

Fishes

The flying adaptation among fishes has occurred at least four times; twice among recent fishes and fully as often during geological times. Dr. O. Abel in the last *Year-book of the Austrian Geological Survey,* describes and figures two ganoid flying-fishes from the New Red Sandstone (Upper Trias). These are Thoracopterus and Gigantopterus and they differ totally from the modern types except in the development of wing-fins for flight. They resemble their non-flying contemporaries in the possession of quadrangular, enamel-covered scales which encased the body.

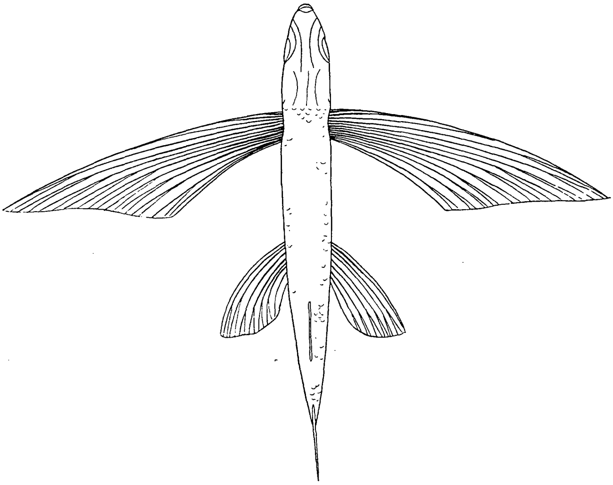

Fig. 1.— *Exocœtus* sp., drawn from an alcoholic specimen. ¼ natural size.

Of modern types two important genera of Teleostomi have acquired flight, Exocœtus, a herring, and Dactylopterus, a gurnard.

Exocœtus.— This genus embraces forty-four species which are generally known as the true flying-fishes in contradistinction to the flying-gurnards or gurnets mentioned above.

In Exocœtus flight modification consists in the elongation and broadening of the pectoral fins and a lesser enlargement of the pelvics as well; so that the weight while in the air is distributed, though unequally, between the two sets of fins as shown in Fig. 1. The anterior fin-rays are much strengthened, especially toward their base, while distally each ray bifurcates to give more support to the flying membrane. The lengthening of the pectoral fins varies with the species, being greatest in those with the best powers of flight.

The bodily contour seems to have suffered but little alteration due to the development of flight. The lower lobe of the caudal fin is much the longer and thus becomes more efficient in giving the fish its final impetus upon leaving the water. It is also said that the fin is occasionally submerged during flight and aids in changing the direction of the fish.

Nearly all of the Scombresocidæ, to which family this flying-fish belongs, have the power of taking great leaps out of the water, culminating in Exocœtus. In the development of the pectoral fin every gradation may be found between the small pectorals of Scombresox *to Exocœtus, Hemiexocœtus being a very remarkable connecting* form (Boulenger).

Exocœtus is tropical to subtropical in distribution, some species having an extremely wide range.

The manner of the flight of flying-fishes has been a much vexed question, one idea being that the creature gets its impetus solely from the tail while in the water, the wings acting merely as parachutes or aëroplanes to support the animal in the air. The other view is that while the initial start is given by the tail, flight is sustained by an actual vibration of the fins as in wing-flapping birds and bats. Some authorities have maintained that the fins move voluntarily only at the beginning and end of the flight, others that this apparent movement is due to an occasional vibration caused by the currents of air.

Colonel Durnford in the January number of the *American Naturalist,* has effectually settled the question by showing that sustained soaring for such a distance (500 feet, Günther) is a mechanical impossibility, due to the moderate initial speed, for a creature of such limited wing-area in proportion to its weight. He further shows that not only is wing vibration necessary, but vibration at extreme speed, such as is invisible to most eyes except at the beginning and end of the flight when the fins are accelerating or retarding their velocity. This is in spite of the statement of Möbius ('78, p. 343) who after examining the musculature as well as watching the living fish came to the conclusion that the fins are not moved at all.

Dactylopterus.— In Dactylopterus the pectoral fins are especially developed for flight and they alone give support to the body in the air as the pelvic fins, which are situated just beneath the pectorals, are not visible from above even when extended. The pectoral fins as a compensation are much broader than in Exocœtus, the relative alar expanse compared with the bulk of the body being much the same in the two genera (compare Figs. 1 and 2).

In the present form the entire body is heavier and of more robust build and the strongly armored head is flattened beneath. The tail in Dactylopterus is symmetrical, not with a larger lower lobe as in Exocœtus.

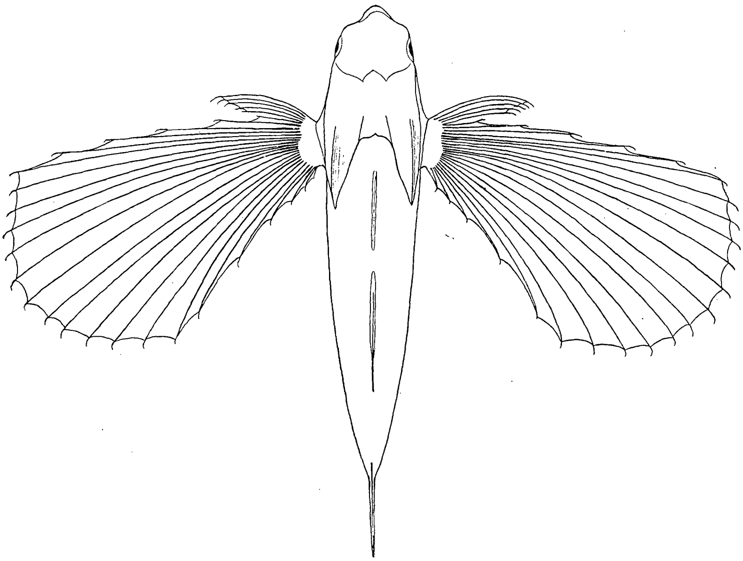

Fig. 2.— *Dactylopterus volitans.* From an alcoholic specimen. ¼ natural size.

The pectoral fins, aside from their greater breadth, differ from those of the latter genus in having more membrane in proportion to the supporting fin-rays, making a less rigid organ. In the young flying-gurnards, formerly thought to represent a distinct genus, Cephalacanthus, the pectorals are so much shorter than those of the adult that they are unable to raise themselves out of the water (Günther).

Moseley ('79, p. 571) says: "I have distinctly seen species of Flying Gurnets move their wings rapidly during their flight . . . . especially in the case of a small species of Dactylopterus with beautifully coloured wings, which inhabits the Sargasso Sea." He further says that he has never seen any species of Exocœtus flap its wings which must be taken as indicating that in Dactylopterus the movement is much slower so as to be distinctly visible. This one would be led to expect from the feebler wing structure and the result is a much less developed power of flight. Moseley likens the flight of the gurnets to that of grasshoppers.

Boulenger (:04, p. 701) recognizes four species of Dactylopterus which are found in "the tropical and warm parts of the Atlantic and Indian Ocean and Archipelago."

AMPHIBIA

The only volant adaptation among the Amphibia is that of the tree frog, Rhacophorus, in which the webbed feet bear the creature up during the prolonged leaps that it takes from tree to tree.

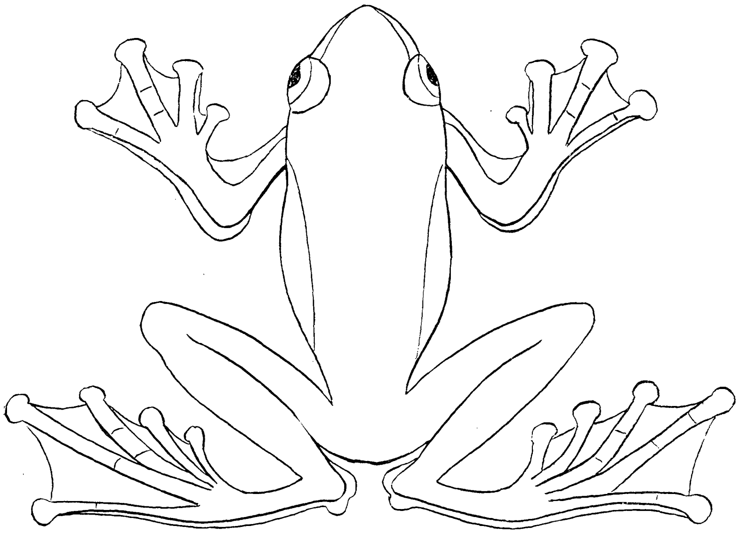

FIG. 3.— *Rhacophorus rheinhardtii.* After Duméril and Bibron. Natural size.

This genus includes more than forty species and has a wide distribution in the paleotropical realm. It was first described by Wallace ('69, p. 38) who evidently through error exaggerated the extent of the supporting membranes very much. The generic name is derived from the presence of the small dermal flaps seen especially at the heel.

The digits terminate in adhesive pads and are connected by web-like expansions of skin which also extends between the two outer metatarsals. Membranes are developed as well in front and behind the arms, rudiments of the prepatagium seen in higher forms.

The figure (Fig. 3), which is modified from that of Duméril and Bibron ('36, pl. 89), is that of *Rhacophorus rheinhardtii* and shows a very conservative development of the parachute, though in the majority of species the web extends not more than half the length of the fingers. In *Rhacophorus pardalis* the total alar expanse is about three square inches (Gadow). This would imply rather feeble soaring powers.

REPTILIA

Reptilia exhibit at least three instances of volant adaptation, the most notable instance being that of the extinct Pterosauria in which true flight was developed, the special adaptation of the entire organism being second only to that of birds.

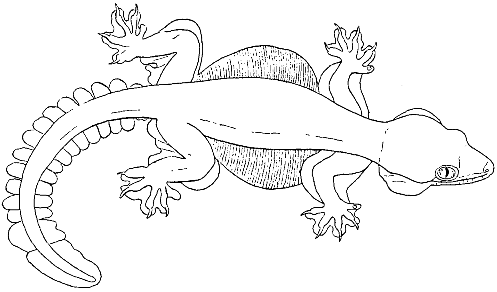

FIG. 4.— *Ptychozoon homalocephalum.* After Duméril and Bibron.

Lacertilia.— Among modern types two lizards have the power of soaring, though in varying degree.

Of these lizards the first is of the family Geckonidæ, *Ptycho-*

zoön homalocephalum, a remarkable form from the Malay Islands and the Malay Peninsula. This creature, shown in Fig. 4, is about eight inches in length, a typical gecko in foot structure, but with membranous expansions along the sides of the head, limbs, body, and tail. The membrane also extends between the digits as in Rhacophorus. The membrane of the tail consists of a series of short flaps on either side. These extensions of the skin seem to be unsupported in contrast to those of Draco, but subserve the same function of supporting the creature in its soaring leaps.

The membranes are discernible in the newly hatched young (Gadow).

In *Draco volans* of the family Agamidæ, the supporting membrane is limited to the sides of the trunk and is of ample extent, well supported by the ribs of which five or six pairs extend beyond the body wall as shown in Fig. 5. The membrane is capable of being closed like a fan against the sides of the body, and its efficiency as a buoyant organ is increased by the concavity of the inferior surface.

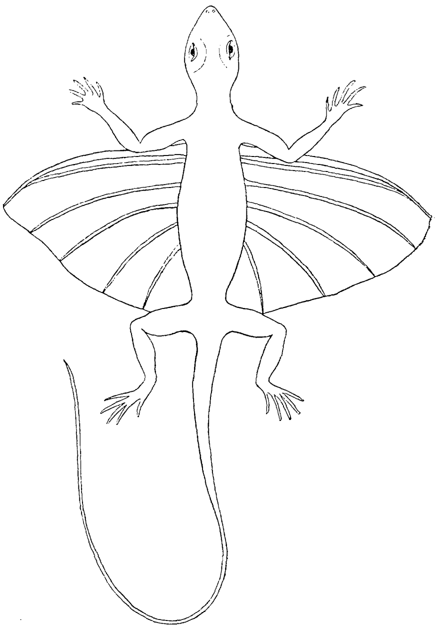

Fig. 5.—*Draco volans.* From a mounted specimen. ½ natural size.

The body is strongly depressed and the tail is extremely long and slender and must aid the creature in guiding its flight.

There are in all about twenty species of Draco, inhabiting the East Indies. The power of flight is not very great, but probably exceeds that of Ptychozoön.

Pterosauria

The pterodactyls were a remarkable group of reptilian forms whose remains are known from the Mesozoic rocks, ranging from the Rhætic to the Upper Chalk. As yet we know nothing of their ancestry, for the first which appear are in every way characteristic of the group.

Seeley (:01, p. 229) says: "There is no geological history of the rapid or gradual development of the wing finger, and although the wing membrane may be accepted as the cause of its existence the wing finger is powerfully developed in the oldest known pterodactyls as in their later representatives.

"Pterodactyls show singularly little variation in structure in their geological history. We chronicle the loss of the tail and the loss of teeth. There is also the loss of the outermost wing-digit from the hind foot as a supporter of the wing membrane. But the other variations are in the length of the metacarpus, or of the neck, or of the head." One might add to this an increase of size as the huge pterodactyl Pteranodon and its allies are among the last to appear.

The adaptation of the pterodactyls for flight is a very perfect one, implying not only the development of true wings, but a specially modified respiratory apparatus coupled with a highly developed pneumaticity of the bones as in birds. There is also a very bird-like modification of the brain which is unlike that of any other reptile. This is seen especially in the width of the hemispheres which touch the well developed cerebellum. On each side of the cerebellum lie the optic lobes while the flocculi, lateral appendages of the cerebellum, which are known elsewhere only in birds, are well developed (Gadow).

Skull.— The skull resembles that of birds, exhibiting large vacuities in some forms and bearing well developed teeth set in distinct sockets and varying in size. In Pteranodon and its allies the jaws were toothless and were evidently not sheathed with horn but with a leathery skin, indicating probably fish-eating habits. Posteriorly, the skull of Pteranodon is prolonged into a compressed, vane-like process evidently not for muscular attachment but to aid in keeping the head pointing into the wind. This would otherwise not only require great muscular effort but would probably have deflected the creature from its course. The head is articulated at right angles with the neck as in birds and in bipedal dinosaurs.

Wings.— The wings consist of the patagium, a broad expanse of membrane, supported by the fore and hind limbs, a prepatagium in front of the arm, and an interfemoral membrane extending between the hind limbs and the tail. The patagium was delicate and very similar to that of the bats. The surface was marked with delicate striæ, which seem to be minute wrinklings. The membrane, when not extended, was thrown into longitudinal folds.

Fore Limb and Girdle.— The skeleton of the fore limb and girdle shows a remarkable modification for the purposes of flight, differing markedly from either the bird or the bat. The pectoral arch is reduced to two pairs of elements, the scapulæ and coracoids, as the clavicles are entirely wanting. In the forms existing before the Cretaceous period the scapulæ are saber-shaped and are united with the coracoids at an angle of less than 90° exactly as in carinate birds. The Cretaceous pterodactyls differ, however, in that the scapulæ, while articulating at right angles with the coracoids, are directed toward the vertebræ uniting with their neural arches. In Pteranodon the scapula articulates with the coalesced spines

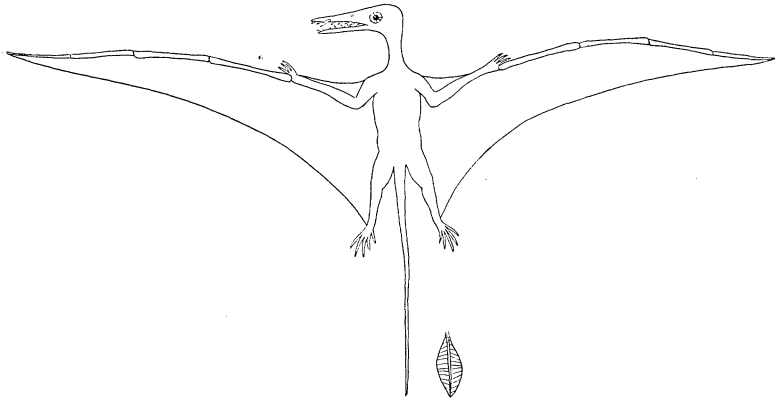

Fig. 6.— *Rhamphorhynchus phyllurus.* Modified from Marsh and Zittel. About $\frac{1}{7}$ natural size.

of several coössified vertebræ, being, as Marsh says, "virtually a repetition of the pelvic arch, on a much larger scale" (Marsh, '82, p. 254).

The sternum is large with a carina or keel, especially in the anterior part, which extends forward in front of the coracoid articulations. The keel is but feebly developed in the great sailing forms like Pteranodon while on the other hand it is very high in Rhamphorhynchus which evidently flew by flapping the wings rapidly. The coracoids unite with the sternum by a true synovial joint.

The most notable feature of the humerus is the form of the proximal articular surface which is saddle-shaped, being concave along the horizontal axis and convex vertically. There is also a remarkable development of the radial crest.

The ulna and radius are nearly of the same size, the latter being somewhat smaller, while of the metacarpals, that of the wing finger is of great size and strength while those of the three preceding digits are very slender bones. The joint for folding the wing is between the metacarpals and phalanges, not at the wrist as in birds.

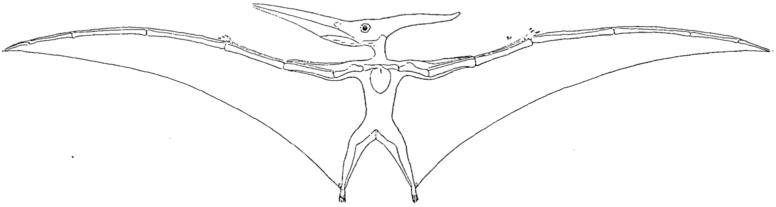

FIG. 7.— *Pteranodon* sp. Modified from Eaton. About $\frac{1}{54}$ natural size.

The number of digits is probably five as there are two bones articulating with the distal carpal on the inner side of the wrist which Marsh ('82, p. 254) interprets as the metacarpal and first phalanx of the first digit. The phalanx, which he calls the "pteroid bone," formed part of the support for the prepatagium, being directed inward toward the shoulder. Others have interpreted this bone as an ossified tendon. If Marsh is correct the number of digits would be five, the fifth being the wing finger.

Hind Limb and Pelvis.— The pelvis is crocodilian in character, while the hind limbs are bird-like with splint-like fibulæ and long, slender tibiæ. The feet have long metatarsals bearing five digits.

In Dimorphodon and other long-tailed forms the outer digit resembles somewhat that of the hand, only on a much smaller scale. It probably also aided in the support of the patagium. In the short-tailed types, on the contrary, this digit is reduced to a vestige without phalanges.

I have figured for comparison two notable genera, the types of which may each be found in the Yale University Museum. Of these, Rhamphorhynchus, representing the suborder Pterodermata Seeley, is a small form from the Solenhofen Slate with a long tail terminating in a peculiar vertical rudder-like expansion supported by neural spines above and by the chevron bones below. This was undoubtedly for steering (Fig. 6).

The other form, Pteranodon (Fig. 7), belongs to the suborder Ornithocheiroidea of Seeley. It is from the Kansas Chalk, a creature with an alar expanse of eighteen feet! Vast in comparison with the diminutive body. In Pteranodon the tail is reduced to a vestige which afforded but little support to the interfemoral membrane. If one may judge from the relation of wing expanse to the size of the body it would seem as though Pteranodon must have had a sailing flight, flapping the wings slowly if at all. It may have been similar to the albatross (*vide supra,* p. 539) in habits of flight, or it may have been unable to fly except on a windy day when, by facing the wind, it would be able to rise to a considerable altitude before its inertia was overcome. Rhamphorhynchus on the other hand was probably a more active flier exhibiting the wing-flapping method of flight.

Birds

The birds form a remarkably homogeneous group reaching the climax of volant adaptation. Flight has, however, been lost in some of the more specialized forms as the penguins among the Carinate birds and in the whole group of so called Ratite birds.

In brief, the modifications for flight consist in the alteration of the fore limb into a wing with a reduced hand and with slightly developed pre- and postpatagiums, but with the alar expanse increased by the development of the feathers. The tail also becomes an efficient steering organ and adds materially to the support of the animal in the air as well. Aside from the bodily conformation which is such as to offer but little resistance to the air in passage, the respiratory organs seem to show the best adaptation to its mode of life of all the other mechanisms of the bird.

A very interesting series of comparisons may be made between the birds and the pterodactyls which must be explained as the result of convergence, though the evidence of a common ancestry for the two groups is very strong. Other characters there are in common with the dinosaurs, explicable in the same way, but these can hardly be said to be volant adaptations as we have no evidence that the dinosaurs acquired flight.

Fore Limb and Girdle.—The fore limb and shoulder girdle are wonderfully adapted to their purpose. In the pectoral arch all three elements are represented in contrast to the coracoid and scapula in the pterodactyls and the clavicle and scapula in the bats. The clavicles have united ventrally to form what is technically known as the furculum which does not always articulate with the sternum. The scapulæ and coracoids fuse with each other firmly, forming in the Carinatæ an angle of less than 90° as in the earlier pterodactyls, while in the Ratitæ the angle formed is greater than 90°, a feature associated with the loss of flight.

The scapula is saber-shaped, and lies parallel with the vertebræ, with which it never articulates as in the later pterosaurs. The coracoid is a massive, pillar-like bone firmly articulated with the sternum. Its duty is to withstand the stress of the great pectoral muscles which would pull the shoulder toward the breast-bone were it not for the resistance offered by the coracoid.

The sternum is large, covering in the Carinatæ much of the ventral wall of the chest and it bears along its midventral line a high keel or carina for the origin of the muscles of flight. In the Ratitæ the keel is wanting, having been lost with the reduction of the pectoral muscles. In pterodactyls the sternum is similarly keeled, though to a less extent, in the smaller forms which had flapping flight. The keel becomes obsolete except upon the forwardly projecting process of the sternum in such huge forms as Pteranodon which, as we have seen, were probably sailers.

In the carinate birds the humerus is notable mainly for the size of the crests which afford attachment for the various muscles. The humerus is reduced in those birds which have lost the power of flight and may be entirely absent as in many of the moas.

Seeley (:01, p. 47) tells us of the remarkable similarity which exists between the foramen in the humerus of the pterodactyl and that of the bird, by which air enters the cavity of the bone. He says: "In the Pterodactyle the corresponding foramen has the same position, form, and size, and is not one large hole, but a reticulation of small perforations, one beyond another, exactly such as are seen in the bone of a bird in which the pneumatic character is found."

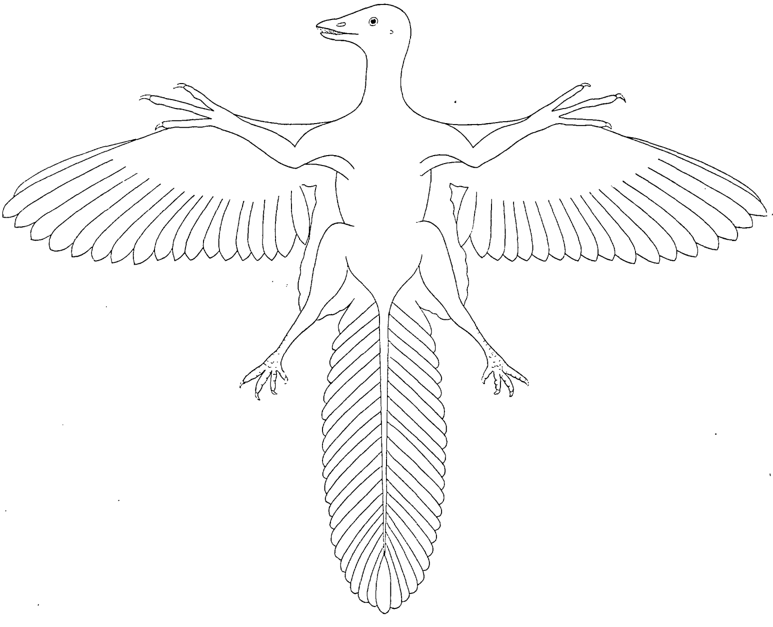

Fig. 8.— *Archæopteryx macroura.*

There are in modern birds but three unequally developed metacarpals which are firmly coössified. The digits are represented by one, or rarely two, phalanges in the pollex which supports the bastard wing, while the second digit, which is much the largest, bears two, and the third one phalanx. Claws are sometimes borne on the first and second digit in modern birds; in Archæopteryx upon the third as well.

Archæopteryx exhibits naturally a more primitive condition of structure than do modern birds, but even here the features are truly bird-like. The sternum is not well known, but the furcula and the coracoids are like those of existing birds. The wing is shorter in Archæopteryx with rather slender bones; the humerus is somewhat longer than the radius and ulna. But one carpal bone is known though at least one other must have existed. The three metacarpals are free and each bore a well developed digit terminating in a claw. We do not know whether the second bore any of the contour feathers as in modern birds or whether they were all borne on the third finger.

Hind Limb and Pelvis.— The hind limb and pelvis of birds can hardly be said to exhibit volant adaptation, unless it be in the development of pneumaticity, as their structure is so closely paralleled in certain of the dinosaurs. It seems rather that the dinosaur-avian type of limb, or the tendency to acquire it, is an inheritance from a common ancestor which certainly could not have possessed the power of flight as the dinosaurs show no evidence of having had and lost this characteristic.

Tail.— The tail of the bird shows a distinct flight modification less developed, however, in Archæopteryx in which the tail was elongated and lizard-like and bore a pair of oppositely placed feathers on each segment. These evidently were used for steering and must have afforded a good deal of support to the body as well, in compensation for the comparatively small wings. The Neornithes or modern birds, on the other hand, have shortened tails, several of the terminal vertebræ having fused to form a pygostyle. Around this vestigial tail the rectrices are arranged fan-wise making a very efficient organ for steering and for checking the rapidity of flight.

A comparison of the figure of the pigeon (Fig. 9) with that of Archæopteryx (Fig. 8) is interesting as showing the increase in the expanse of the wings to compensate for the reduction of the tail so that the relative buoyant surface remains approximately the same.

The Trunk.— The rib structure of the Neornithes must be considered as a definite flight modification for here only do we find the sternal and vertebral ribs articulating by a true synovial joint. This, together with the elbow-like flexion of the joint, forms an admirable mechanism for the dorso-ventral increase and decrease of the chest cavity during respiration. When the bird is resting the back is rigid and the sternum moves, but during flight when the sternum is supporting the creature it is the back which rises and falls.

The long slender neck and the tendency on the part of the trunk vertebræ to coössify, are further skeletal characteristics of birds.

Respiratory Organs.— While all of the nutritive organs are necessarily larger and more efficient in birds as the direct result of more rapid expenditure of energy during flight, the respiratory organs show the most remarkable adaptation. The lungs are inelastic and do not hang freely in the cavity of the chest as do those of mammals, but are connected with an extensive series of air sacs, principally in the abdomen, but in other portions of the body as well. These serve not only to lighten the specific gravity of the bird, but, by means of the abdominal sacs, air is drawn *through* instead of merely into the lungs with the result that the air in the latter is entirely renewed with each inspiration. There being thus no residual air, the entire lung functions for the aëration of the blood. The respiratory system is further connected with the cavities within the bones as in pterodactyls and while this pneumaticity is evidently an aid to flight as it reaches its maximum development in such powerful fliers as the pelicans, it is on the other hand but little

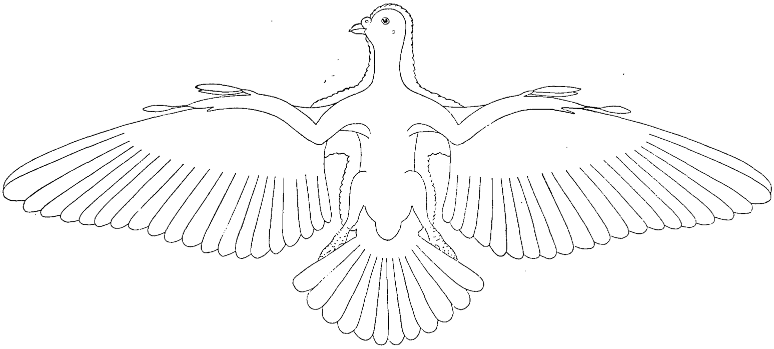

FIG. 9.— *Columba livia.* Modified from Parker and Haswell.

developed in the gulls which are also strong of wing. Seeley says: "Comparison shows that in so far as the bones are the same in the bird and ornithosaur, the evidence of air cells entering them extends to resemblance, if not coincidence in every detail. No living group of animals except birds has pneumatic limb-bones, in relation to the lungs; so that the identical structures in the bones were due to the same cause in both living and extinct groups of animals" (Seeley, :01, p. 50).

Brain.— In the avian brain the convergence[1] toward that of the pterodactyl lies in the position of the optic lobes which are laterally displaced so that the cerebrum may extend between as well as over them in order to abut against the cerebellum. There is also a similarity in the development of the lateral lobes or flocculi upon the sides of the hind brain. These features seem to be adaptations correlated with the development of flight.

Mammalia

The Mammalia show at least eight distinct flight evolutions. In seven instances soaring has been developed as an aid to prolonged leaps, while the Chiroptera as an order are true fliers. This should not surprise us for all but one of the forms are arboreal and with arboreal types the development of parachutes for sustaining the creature in the air during its passage from tree to tree is a logical course of evolution.

Marsupialia

Among the marsupials of the family Phalangeridæ there are three genera, Petauroides, Petaurus, and Acrobates, which have independently acquired the power of soaring; for the three genera are each in turn especially related to a separate type of non-flying phalanger. The same observation can be made about the flying squirrels, Anomalurus and Sciuropterus (Beddard).

---

[1] Dr. F. B. Loomis is of the opinion that the brain similarity is due to real relationship and is not a convergence. He explains in the same way the similarity of the openings into the pneumatic bones.

In all of these forms the flight adaptation consists mainly in the development of a horizontal fold of skin (the patagium) stretched along the sides of the body between the fore and hind limbs.

Petauroides.— In Petauroides the flying membrane extends from the wrist to the ankle, but is very narrow along the lower segment of each limb. The tail is very bushy except for its prehensile tip which is naked inferiorly, and, together with the long fur which clothes the body, must aid considerably in buoying the creature up while soaring.

Petauroides includes but a single species, *P. volans*, the so called Taguan flying phalanger, found in Australia from Queensland to Victoria. Its nearest ally is Dactylopsila which, however, has no flying membrane but has the same partially naked tip to the tail.

Petaurus.— Petaurus has a much broader patagium which extends from the outer finger to the tarsus; there is also a slight extension of membrane in front of the fore limb. The tail is very large and evenly bushy, lacking the naked tip. This genus contains three species which are somewhat smaller forms than Petauroides. They seem to have been derived either from the genus Gymnobelideus, which resembles Petaurus closely except that it is flightless, or from an allied extinct form (Lydekker).

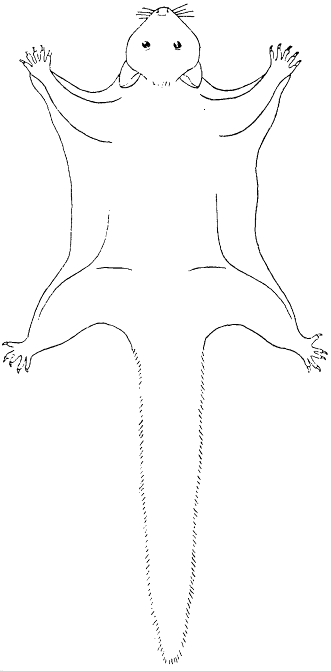

FIG. 10.— *Petaurus sciurius.* Modified from Flower and Lydekker.

The geographical range of Petaurus is "over New Guinea and part of Australia, including the area from the Halmahéra group of Islands to Victoria."

Acrobates.— The third genus, Acrobates, contains two species of which the individuals are of small size with a narrow patagium extending from the elbow to the knee along the flank. The buoyant area is increased, however, by the long fringing hairs. There are striated pads at the extremities of the digits. The probably prehensile tail has its long hairs arranged on either side as in its near ally, the pen-tailed phalanger, Distæchurus, which from its skull and teeth may be very close to the ancestral type of Acrobates.

One species, *Acrobates pygmæus*, is found in Queensland, New South Wales, and Victoria and the other, *A. pulchellus*, in Papua, while Distæchurus is now found in New Guinea. Acrobates is extremely active with great soaring powers.

Rodentia

Two families of rodents, the Anomaluridæ containing but one flying genus Anomalurus, and the Sciuridæ containing among others the flying genera Pteromys, Sciuropterus, and Eupetaurus, have developed the power of soaring by means of a patagium.

These families represent in each case a distinct adaptation to volant life, though the three genera of the Sciuridæ are closely related and are not as in the Phalangeridæ, related each in turn to a non-flying ally. The convergence of the flying rodents toward the flying phalangers is very marked though the former are apt to develop more or less of a prepatagium and an interfemoral membrane in addition to the patagium along the flanks. This is, however, as will be shown, a variable feature.

Anomalurus.— The Anomaluridæ include three genera of which Anomalurus with six species is the most important. In this genus the patagium is well developed and is supported by a cartilaginous process of the olecranon. The membrane extends from the carpus to the tarsus but narrows along the front of the leg from the knee down. This is compensated for by an interfemoral membrane from the heel to the tail a little beyond its base.

A distinctive feature of these forms, while not a volant adaptation but rather an arboreal one, is the presence of imbricated, keeled scales beneath the tail which apparently aid in climbing. The tail is not very bushy so that it probably aids but little in flight.

Anomalurus resembles Pteromys but is distinguished therefrom and from Sciuropterus by the caudal scales and by the position of the supporting cartilage. Anomalurus is African in habitat.

The allied genus, Idiurus, differs in minor details from Anomalurus, while Aëthiurus from the French Congo, has no flying patagium.

Pteromys.— Among the Sciuridæ, Pteromys has a patagium extending as far as the digits and supported as in Anomalurus, by a cartilage, but one arising from the carpus rather than from the olecranon. In addition to the interfemoral membrane extending to the root of the tail, there is also a narrow prepatagium running from the anterior limb to the sides of the cheeks. The tail

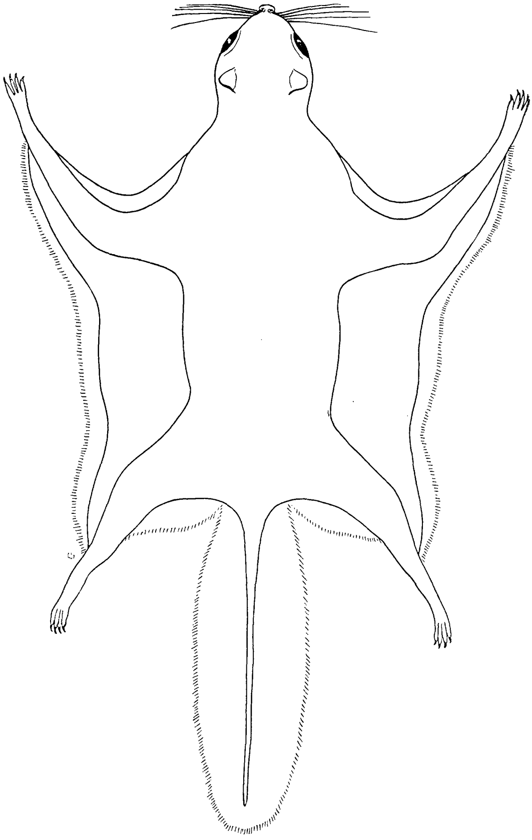

FIG. 11.— *Sciuropterus volucella.* From a mounted specimen. ½ natural size.

is larger than in Anomalurus and must add materially to the support of the body in the air. It is said that Pteromys can soar through a distance of nearly eighty yards, depending of course upon the initial altitude above the ground.

Pteromys is found in the "wooded districts of tropical southeastern Asia, Japan, and some of the Malaysian Islands" (Heilprin).

Sciuropterus.— Sciuropterus, which is here figured (Fig. 11), has no interfemoral membrane, but as a compensation, the tail is much more fully developed than in Pteromys. In the latter it is round and comparatively thin while in Sciuropterus the tail is flat and broadly expanded. A hairy fringe extends beyond the margin of the patagium and behind the femora as well, thus extending the supporting area as the figure clearly shows.

Sciuropterus includes smaller forms than Pteromys, but its range is much more extensive as it includes the northern part of North America and the Eurasian continent.

Eupetaurus.— Eupetaurus resembles Pteromys but has no interfemoral membrane. It differs from the preceding forms mainly in having hypsodont teeth rather than brachyodont which implies a difference in feeding habits. Eupetaurus is rock- and precipice-inhabiting rather than arboreal and inhabits the high elevations of northwestern Kashmir.

Insectivora

Among the Insectivora, Galeopithecus stands alone in its volant adaptation for it shows the greatest specialization for flight of any of the Mammalia except the bats. Indeed Galeopithecus, while too specialized to be ancestral to the Chiroptera, is evidently from a common stock and gives us a pretty clear idea of the characters of the forms from which the latter arose.

In Galeopithecus, which is an animal of considerable size, the patagium is well developed and is supplemented by a prepatagium and an interfemoral membrane which includes the entire tail precisely as in the insectivorous bats. The patagium is well supplied with muscles and nerves which are homologous with those in the wing membrane of the Chiroptera and differ decidedly from those of the other volant Mammalia.

The hand is much larger than the foot and the flying membrane is continued along the side of each as well as between the digits, and while the fingers show no trace of the elongation so characteristic of the bats, if such were to occur the result would be a very bat-like structure.

Galeopithecus is unique in the character of the teeth which are adapted to a phytophagous or leaf-eating habit, while the alimentary canal resembles that of the Chiroptera except that in Galeopithecus the colon is long, while in bats as in birds the colon is very short. This shortening of the colon is clearly a volant character due to the freedom with which excrement may be voided by aërial forms and the consequent lack of necessity for a place of storage of effete matter.

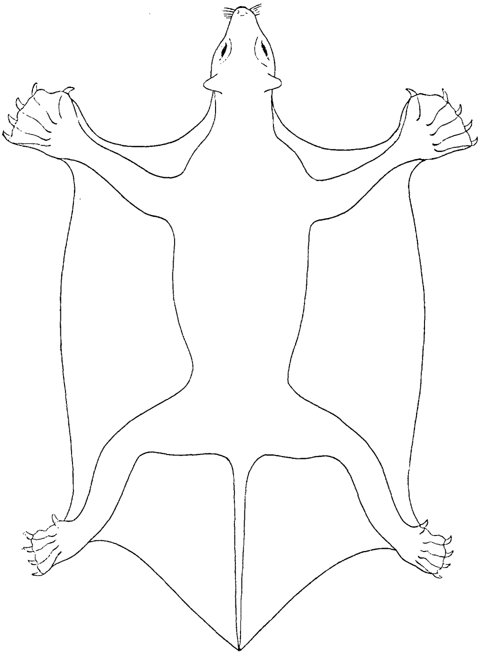

FIG. 12.— Galeopithecus. Modified from Wood.

The brain in Galeopithecus is midway in its development between that of a typical insectivore and that of a bat.

Galeopithecus is nocturnal in habits, as indeed almost all volant mammals are, resting during the day by clinging head downward from the branch of a tree, in which posture it resembles Pteropus very closely. Its soaring powers are very great as one has been seen to cover a space of seventy yards with a descent of not more than thirty-five or forty feet, or less than one in five (Wallace).

Two species of Galeopithecus are known, one, *G. volans*, from the Malay Peninsula, Sumatra, and Borneo, while *G. philippinensis* inhabits the Philippine Islands.

Chiroptera

In the bats one sees the culmination of volant adaptation on the part of the Mammalia and the entire order has reached a state of perfection excelled only by the birds and pterodactyls. Each of the three solely air-breathing classes of vertebrates has, in one line of evolution at least, culminated in perfect adaptation to aërial life.

The bats while showing the same general plan of structure throughout, are divisible into two distinct suborders in which constant distinguishing characters have arisen, due to differences of habits. These are the Microchiroptera and the Megachiroptera, the former being in the main insectivorous while the latter are frugivorous in habits. Each group, however, contains some aberrant forms.

The Patagium.— The most notable volant characters are the great development of the digits of the hand supporting the patagium which extends along the sides of the body and hind limb to the tarsus. There is a well developed prepatagium extending from the neck to the wrist. An interfemoral membrane is also present, but varies in development in the two suborders, including the somewhat elongated tail in the Microchiroptera, while in the tailless Megachiroptera each membrane is a triangular area meeting its fellow at the end of the spine. In the Microchiroptera the membrane is further supported by a cartilaginous rod, the calcar, arising from the heel and directed obliquely inward toward the tip of the tail. The development of the tail gives, with the interfemoral membrane, an efficient organ for steering and checking the way of the animal during flight, so necessary in the pursuit of insects and which gives to the twilight bat its characteristic flight. It is also said that this structure is of use in the capturing of prey.

In the vampire and other aberrant carnivorous Microchiroptera, there is no tail, a point of agreement with the frugivorous forms. The tailless bats are much heavier fliers as a rule, flapping their way slowly through the air.

The patagium is naked, being clothed with hair along the sides of the body only, and the surface of the integument is finely wrinkled as in the pterodactyl Rhamphorhynchus. The method of folding the wing when at rest is also the same. The contrast between the wing of the bat and that of the pterodactyl is in the support of the membrane in the former by four digits, only the pollex being free, while in the latter the outermost finger alone supports the wing membrane. The contrast with the bird lies in the reduction of the digits in the latter to three and in the retrogression of the patagium whose place as a buoyant surface is taken by the feathers.

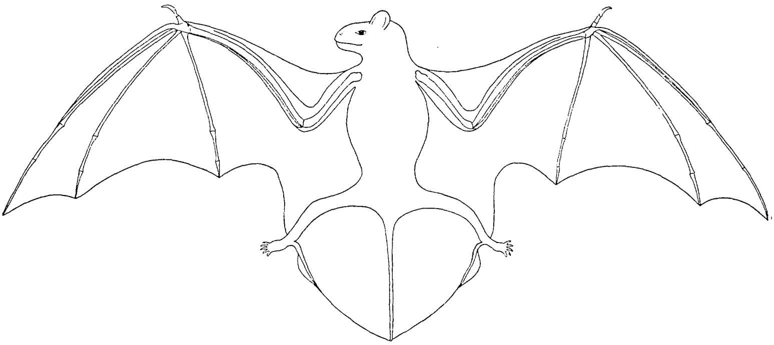

FIG. 13.— *Vespertilio noctula.* Modified from Flower and Lydekker.

The Fore Limb.— The pollex is always free and clawed and aids in crawling on level ground, but more especially in climbing. In the Microchiroptera the second finger while distinct is not free but is attached to the third distally so that the two together support the anterior margin of the wing. The third finger, however, is much the longest and digits four and five are well developed and free.

In the Megachiroptera the contrast lies mainly in the difference in wing proportions due to the fact that the second digit is free from the third and supports a portion of the patagium alone. It is further clawed at the tip. A comparison of Figs. 13 and 14 will render these distinctions clear.

The bones of the wing are very slender with large, medullary cavities, but without any trace of pneumaticity as in birds and pterodactyls. The shoulder girdle, consisting of well developed clavicles and scapulæ, is very strong. The clavicles are curved and the scapulæ bear strongly curved coracoid processes. The humerus is well developed but is much exceeded in length by the radius which is a strong, curved bone while the ulna is much reduced.

The Hind Limb.— One chiropteran peculiarity which is clearly a flight adaptation is the backward rotation of the hind limb so that the knee points towards the rear instead of toward the front as in quadrupeds. This feature is a distinct disadvantage for terrestrial locomotion, making the creature extremely awkward when upon the ground.

There are five compressed digits in the pes bearing long, curved claws and used as in Galeopithecus for suspending the creature head downward when at rest.

The Trunk.— The chest is remarkably capacious to contain the large lungs and heart which resemble those of birds in their state of development.

The vertebral column is short owing to the compact form of the body and the individual vertebræ have but little movement and tend to coössify in old age. The neural canal is largest in the cervical and thoracic regions, rapidly diminishing toward the rear. This is due to the large size of that portion of the spinal cord from which the great muscles of flight are innervated as contrasted with the feeble development of the posterior portion of the body.

The presternum has a well developed keel as in birds and pterodactyls for the origin of the muscles of flight.

The Brain and Sense Organs.— While the brain of the Chiroptera is of as lowly organization as the most nearly allied order, the Insectivora, certain senses of the bats, especially that of touch, have undergone a remarkable degree of development and refinement. This tactile sense seems to reside mainly in the vibrissæ, in the wing membrane, and in the ear pinnæ which in some types are very large. More especially is the sense developed in the leaf-like expansions of the skin about the nose and face in the Rhinolophidæ and Phyllostomatidæ. These appendages are the seat of so delicate a sense of touch that actual bodily contact with an object is not necessary to its perception, but the reflected aërial waves suffice to stimulate the sense organ. This is a notable secondary flight adaptation, not useful as a direct aid to flight, but in guiding a rapidly moving nocturnal flier it must prove invaluable.

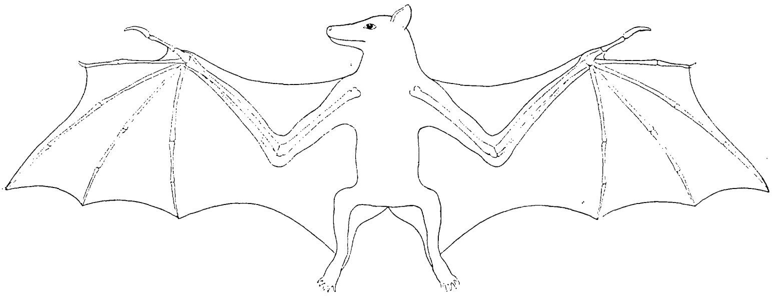

FIG. 14.— *Pteropus* sp. Modified from Owen.

The Chiroptera are practically world-wide in distribution, being found wherever sufficient food may be procured.

Primates

Among the primates one genus exhibits a small patagium which aids in soaring. This is the genus Propithecus of the family Lemuridæ.

In these forms the power of flight is somewhat limited. Flower and Lydekker give ten yards as the length of the leap, attributing the soaring to the powerful hind limbs, without even mentioning the existence of the patagium. Beddard on the other hand speaks of the "parachute-like fold of skin between the arms and the body which suggests the more complete parachute of Flying Foxes, etc."

Propithecus includes three species, all from the Island of Madagascar. They are diurnal, contrary to the general rule among volant mammals, though they prefer the morning and evening for their periods of activity.

Summary

1. Volant evolution has occurred seventeen times among vertebrates, ten of which are merely adaptations for more or less prolonged soaring leaps, while in seven instances in all probability true flight has been developed.

2. Soaring implies, with but one exception, the development of a fold of skin along the creature's flanks supported in one instance by the extension of the ribs beyond the body wall, but generally stretched between the fore and hind limbs. This fold is often supplemented by others in front of the fore limbs and between the hind limbs sometimes involving the tail.

3. True flight always implies a more or less profound modification of the fore limbs which become, as a consequence, unsuited to ordinary progression. True flight has been developed once in each of the classes of strictly air-breathing vertebrates, and probably at least four times among fishes.

4. With the exception of the fishes, soaring implies also present or ancestral arboreal adaptation and this may apply as well to the true fliers. It is certainly true of the bats, possibly true of the birds, but of the pterodactyls one cannot be certain.

5. Besides the primary modifications which constitute the machinery of flight, other portions of the body, especially the nervous system, the sense and the nutritive organs, may exhibit secondary volant characteristics. These, as with the primary modifications, are in direct proportion to the powers of flight.

Amherst, Mass.

BIBLIOGRAPHY

Abel, O.

: 05. Year Book of the Austrian Geological Survey.

Beddard, F. E.

: 02. Mammalia. *The Cambridge Natural History,* vol. 10. London.

Boulenger, G. A.

: 04. Fishes. *Cambridge Natural History,* vol. 7. London.

Chapman, H. C.

: 02. Observations upon *Galeopithecus volans. Proc. Acad. Nat. Sci. Phila.,* vol. 54, pp. 241–254.

Duméril, A. M. C., et Bibron, G.

'36. Erpétologie générale ou histoire naturelle complète des reptiles. Paris.

Durnford, C. D.

: 06. Flying-fish Flight, and an Unfixed Law of Nature. *Amer. Nat.,* vol. 40, pp. 1–11.

Eaton, G. F.

: 04. Characters of Pteranodon (Second Paper). *Amer. Journ. Sci.,* ser. 4, vol. 17, pp. 318–320, pls. 19–20.

Flower, W. H., and Lydekker, R.

'91. An Introduction to the Study of Mammals Living and Extinct. London.

Gadow, H.

: 01. Reptilia and Amphibia. *Cambridge Natural History,* vol. 8. London.

Günther, A. C. L. G.

'80. An Introduction to the Study of Fishes. Edinburgh.

Heilprin, A.

: 01. The Geographical and Geological Distribution of Animals. New York.

Lydekker, R.

'94. A Hand-book to the Marsupialia and Monotremata. London.

Marey, E. J.

'79. Animal Mechanism: a Treatise on Terrestrial and Aerial Locomotion. New York.

Marsh, O. C.

'82. The Wings of Pterodactyles. *Amer. Journ. Sci.,* ser. 3, vol. 23, pp. 251–256, pl. 3, 2 figs.

Marsh, O. C.

'84. Principal Characters of American Cretaceous Pterodactyls. *Amer. Journ. Sci.,* ser. 3, vol. 27, pp. 423–426, pl. 15.

Möbius, K.
'78. Die Bewegungen der fliegenden Fische durch die Luft. *Zeitschr. f. wiss. Zoöl.*, vol. 30, suppl., pp. 343–382, pl. 17.
Moseley, H. N.
'79. Notes of a Naturalist on the Challenger. London.
Sedgwick, A.
:05. A Student's Text-book of Zoology, vol. 2. London.
Seeley, H.
:01. Dragons of the Air. New York.
Wallace, A. R.
'69. The Malay Archipelago. New York.
Zittel, K. A. von.
'90. Handbuch der Palæontologie, Palæozoölogie, vol. 3. München und Leipzig.